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The Trap of Utricularia

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> 'If a man can write a better book, preach a better sermon, or make a better mouse-trap than his neighbour, though he build his house in the woods the world will make a beaten path to his door.'
>
> —Attributed to Emerson.

Carnivorous animals capture their prey by swiftness or by cunning. While most rely upon speed others are constrained to set traps for the reception of the victim. The Ant-lion (*Myrmeleon*) with its sand-pit, many Spiders with their webs and Man are examples. The last may be termed a facultative trap-setter and the victim may or may not serve as food.

Plants on the other hand lead sedentary lives and are not as a rule adapted to a diet of flesh. There are, however, exceptions—plants that feed upon animals—a fact that has moved someone, somewhere, to poetry:

'What's this I hear
About the new Carnivora?
Can little plants
Eat bugs and ants
And gnats and flies?
A sort of retrograding;
Surely the fare
Of flowers is air,
Or sunshine sweet:
They shouldn't eat,
Or do aught so degrading.'

'Bugs and ants and gnats and flies,' mosquito larvae, oligochaete worms, copepods and soforth are acceptable to these retrogrades. In all cases the plant—be it *Drosophyllum*, the 'flypaper' plant of Portugal, or *Dionaea* of South Carolina with its wonderful 'steeltrap' leaves—sets forth its traps and waits for its prey; which brings us to a consideration of traps in general and in particular to those of the plant that Goebel has been quoted as declaring the most wonderful plant of all.

What should we expect of a trap? In order to be effective it should be well located or failing this should be made attractive to the victim. Of location we shall have more to say below: of attraction much might be written. Thus, in the case of the Sundew, the leaves, deadly though they are, are supposed to attract by virtue of their appearance. The colouring of *Sarracenia,* it is suggested, may have this function.

Traps, like jails, must prevent escape unless (and this happens rarely) the victim is killed at once. It is probable in the case of the Venus flytrap that the psychology of the fly alone renders the trap effective, for the struggles of the insect, by acting as a repeated stimulation, seems to prevent opening of the trap.

Additional merits would consist in a self-setting mechanism and a selective capacity for the rejection of unsuitable material. This last, perhaps, is expecting too much, but we shall see.

In the tropical and temperate regions of the earth are to be found the more than two hundred species of the genus *Utricularia* —the Bladderworts—flowering plants that inhabit a wide variety of situations. Some are epiphytes in the rain-forests of the tropics, others affect more lowly stations and grow on moss and humus. Others again, including all the species of the temperate zones, are aquatics and the flowering stems alone appear above water to bear the showy blue, yellow or white flowers. In one remarkable case the plant lives only in the water collected in the bases of the leaves of a large *Tillandsia* and Gardner (1846) tells us: '. . . propagates itself by runners, which it throws out from the base of the flower stem; this runner is always found directing itself towards the nearest Tillandsia, when it inserts its point into the water and gives origin to a new plant, which, in its turn, sends out another shoot; in this manner I have seen not less than six plants united.'

It is an aquatic species of the North Temperate zone—*Utricularia gibba* L—that is the subject of the following description.

This plant is widely dispersed in North-Eastern America. It grows entirely submerged during the greater part of the year, lifting but its flower stems with their bright yellow blooms three or four inches above the water. The submerged stems are slender and flexuous; their diameter scarcely a quarter of that of an ordinary pin. They may exceed a foot in length. At intervals of one quarter to one half of an inch appear the so-called leaves; structures more slender still which not infrequently branch and which may be, as on the specimen before me, a third of an inch in length. The tip of the stem is inrolled so that it looks rather like a young fern-frond. Both leaves and stem are green and share the work of assimilation.

Near the leaf base and shortly stalked, is to be found the bladder or utricle which is responsible both for the technical and common names. It may be almost colourless, delicately green or with age dark blue, but even in the last case is fairly transparent. The wall of the bladder is of two layers and it is anthocyanin dissolved in the cell-sap of the inner of these that gives the blue colour to old bladders. Nothing of the nature of a root is to be found. Viewed against a dark background, as under natural conditions, we see the picture represented in figure 1.

Let us consider now the bladders for it is to the possession of these that *Utricularia* owes its position of supreme interest.

The bladder has approximately the bulk of a pin's head. Viewed from the side it is pear-shaped, two long, branching antennae (the term is Darwin's) gracing the narrower, forward end and forming wing-fences, as it were, to the vestibule. In order fully to understand the origin of the latter structure we must remember that the forward end of the bladder is closed by a door which is situated well back in the mouth of the trap. The walls anterior to this form the vestibule.

We have said that the main walls of the utricle are of two layers. One should qualify this by adding that two regions are exceptional, the first in having a prolongation of the vascular tissues of the stalk along the ventral and dorsal parts of the bladder, the second in that it forms a relatively rigid and massive 'doorstep' immediately under the door (figs. 2, 3 and 5). Unlike most doorsteps this structure does not end abruptly on either side but merges gently into the lateral walls in a long upward sweep. The cells composing it are larger than any of the other cells. Its upper surface has a curious structure which has led us to refer to it somewhat facetiously as the doormat (fig. 2); of this more beyond.

A close examination of the door reveals its rather complex and entirely surprising nature. It must be studied *in situ* in order to understand its functioning for its shape when injured is very different from that of the living door. It is attached to the walls of the bladder along perhaps two thirds of its periphery—making a hinge that takes the form of a wide arch composed of the top edge and the upper curves of the lateral edges. The doorstep, it will be remembered, merges into the lateral walls and its upper limits are found to coincide with the lower limits of this hinge. The edge of the door is free, then, for approximately the length of the doorstep. The door is not a plane structure but presents a convex face to the outside. This convexity is communicated to the free edge and results in the rather curious path followed by it. Let us consider this in some detail for it is here that recently discovered facts throw light on a mechanism that has intrigued botanists for seventy-five years.

We have first to describe the general mechanics of the trap. It is easy to see that the bladders of a plant differ in shape one from another and we may distinguish three distinct states. Thus, in figure 4 the same trap is shown as it appears at different times. The middle photograph represents it with the lateral walls showing a slight dimpling. In the course of half-an-hour or so this concavity had increased considerably giving the trap the shape figured to the left. The remaining photograph was taken after the bladder wall had been pricked with a fine needle. Czaja (1922-4) and Merl (1922) noted these changes in form.

It is wise before considering the significance of these changes to continue observation of bladders under natural conditions. The small animals that may be found in the pools inhabited by *Utricularia* frequently enter the vestibules of the bladder and move about in it in a manner that suggests the presence of some attractive substance. If the trap is in the markedly dimpled condition a surprising sequence of events follows. There is a momentary commotion and then we may see one or more animals within the trap, their escape prevented by the closed door, and the walls of the bladder are observed to have resumed the position shown in the middle photograph of figure 4. If, now, we prick the wall the utricle expands instantly to the form pictured in figure 4C and remains expanded.

The extreme rapidity of the trapping is made evident by a motion picture, two successive frames of which are shown in figure 7. It will be seen that in the upper photograph a worm is outside the trap: in the lower the greater part of it is within. It happened in this case that the worm was about to divide and when the trap was sprung division was completed, one portion of the worm entering, the other remaining outside!

It is not necessary to wait for an animal to spring the trap: we may use the tip of a fine needle for the purpose. If the bladder is detached from the plant and a slender glass rod is presented to it, it will swallow it, actually jumping at anything that trips the mechanism (figure 8) as observed by Czaja (1922a). We are driven to the conclusion that an inrush of water carries the prey into the trap. If tripped in air the bladder will swallow a bubble of it (figure 6). When plants are lifted from the water it is usual to find that many of the bladders contain air—the traps are sprung as the water flows from the plant. Ekambaram and Brocher actually heard the clicking sound made by the springing traps.

We are now in a position to consider the facts related above. There are two possible 'explanations' of the inrush of water. It might be supposed that sudden turgor changes in the cells of the lateral walls cause them to become less concave. Such a change would not be unique for their are many cases recorded of just such an alteration of turgor. The evidence, however, is all in favour of the view that water is pumped out of the bladder during the transition from the tripped to the set condition. It has been shown that a tiny hole in the wall of the trap or the insertion of a fine bristle under the edge of the door is sufficient to prevent the setting of the trap (Czaja).

If there is indeed a pumping out of water leading to a 'negative pressure' within the utricle it is necessary to assume that the door is water-tight or that any leakage that occurs is so slight as to be unimportant. When traps in the set condition are placed in water containing india ink no leakage can be detected. We have watched such traps for days and in no case have we seen leakage or noticed an automatic springing of the mechanism.

It is now proper to return to a further consideration of the door with a view to understanding how it is rendered water-tight. We have remarked already that the free edge of the door follows a curious course. It starts on either side where the rear edge of the doorstep merges with the lateral walls and traverses the sloping portions of that structure. Its central portion lies just in front of the doorstep.

That this of itself would form a water-tight joint has seemed improbable and careful observation has revealed the presence of a thin, almost transparent 'veil' immediately before the door and following closely the anterior edge of the doorstep (figures 2, 5 and 10) (Loyd, 1929). Although the free edge of the door starts at the rear edge of the latter the door itself bulges against the veil throughout its length and possesses triangular wings that are closely applied to the lateral parts of the doorstep. In these facts we have, to my mind, a possible explanation of the observed fact that the trap when sprung is not usually distended to the utmost (refer to figure 4). If the veil functions as a valve it would seem that a certain difference of pressure between the interior of the bladder and the outside water is necessary to keep it closely pressed to the door. There is a difference of pressure when the trap is in either the set or the sprung state and it is only when the door is held open or when the bladder wall is pricked that pressure equilibrium seems to exist.

Such an explanation may appear fanciful but we must remember that the mechanism must approach perfection before it can function in the manner observed. It is interesting to notice that even this remarkable trap fails on occasion and the victim is jammed in the entrance (figure 9). When this happens the trap is unable to function.

The tripping of the mechanism, leading to the opening of the door and the resultant inrush of water, is brought about, as far as we can tell, by depression of the trigger hairs which project from the door. Immediately above the point of attachment of these bristles is a thin, easily flexed region of the door and it seems likely that a downward movement of the hairs results in a bending of the door at this point and the lifting of the central portion of the edge from its position before the doorstep. The inrush of water then opens the door but it closes again before equilibrium can be attained. How else explain the fact that the bladder in the tripped state can still take in water?

There remain to be described the varied hairs that decorate almost all parts of the bladders. Observation of these reveals the fact that they all are built upon the same general plan, having three cells as the fundamental unit. These may be termed basal, stalk and head cells. On the outer parts of the trap the hairs are very short and deeply sunken. In the porch they are long and slender and on the door itself they are different again. (Withycombe 1924).

Within the trap are hairs of two kinds. Scattered over the wall are the so-called quadrifid hairs which have heads composed of four radiating cells. It is supposed that these are digestive glands or that they absorb water from the cavity and help to pass it to the outside (figure 12). The other hairs are similar but are bifid and are restricted to a limited area on the slope of the doorstep that faces the cavity of the bladder. The upper surface of the step itself (the 'doormat') is a closely packed layer of modified hairs and it is the cuticle of these that forms by exfoliation the veil that is adpressed to the door edge (Lloyd) (figures 2 and 3).

We cannot doubt the power of *Utricularia* to kill and digest its prey for we have seen time and again the death and digestion of oligochaete worms and other animals. Death follows capture relatively quickly, varying enormously, however, from trap to trap and taking place most quickly, as far as our observations go, when the victim is an oligochaete worm. As an example of the rapidity with which the trap may repeat its feats we will quote but a single case. A trap was observed to catch a large worm and was placed on one side that we might watch the process of digestion. We were surprised to find, after a lapse of thirty-five minutes, that the bladder had captured a second, equally large victim.

Death of a worm may take place in a couple of hours and in less than a day nothing but a small amount of detritus remains. The process is far too rapid for bacterial action to be responsible for the change.

This description has been confined almost in entirety to facts and we pass now to the realm of history, fancy and speculation. There is scope enough here as even a casual glance at the literature will show.

While it is possible to observe in a short time all the facts related above we must remember that it is the work of many men that has taught us to observe the traps and correctly to interpret our observations.

The earlier investigators failed to grasp the significance of the bladders. Thus we find that the Crouan brothers (1858) thought them protective devices and regarded the quadrifid hairs as root-hairs. To others the bladders were flotation organs and Darwin (1875) occupied himself for a while in disproving that possibility.

No fewer than four people, as Skutch (1928) reminds us in a recent review, discovered independently that the trap is an active mechanism. These were Brocher of Belgium (1911), Ekambaram in India (1916), Withycombe in England in the same year and lastly Hegner in the New Yorld in 1925. Darwin himself more than fifty years ago came within a hairsbreadth of making the same discovery!

The catholic taste displayed by *Utricularia* has intrigued many and the literature is full of references to the variety of organisms trapped. Among the most interesting observations in this field are those of Goebel (1889) and it will be not inappropriate to select one from the many. *Utricularia intermedia* and *U. vulgaris* when grown together caught quite different animals, the former securing *Cypris,* the latter Copepods. Goebel connected these facts with the observation that *Cypris* is a creeping form and is therefore more likely to meet with the rooted *U. intermedia,* while the freely floating *U. vulgaris* is well situated to trap the swimming copepods.

Hegner (1926) records the capture of Paramoecia: we on the other hand, have not seen this with *Utricularia gibba.* This may be due to some slight differences that prevent our plants from trapping Paramoecia. He would be a brave man, though, who would draw any conclusions from the negative results of observation for no less than seventy-five years of observation passed before Lloyd recorded the veil which seems to seal the door, and it was but twenty years ago that Brocher observed the springing of a trap!

We might speculate along a dozen lines without exhausting the field. We know nothing of the method by which water is pumped out of the traps. What are the digestive enzymes of the bladders and is secretion stimulated when animals are trapped? Is the *Euglena* that inhabits old bladders immune to these enzymes or are such old traps no longer functional?

In spite of the work of the investigators quoted, together with that of Buesgen, Cohn and others, we have before us today, in a modified form, to be sure, what Brocher nearly twenty years ago called 'Le Probleme de l'Utriculaire.'

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DESCRIPTION OF FIGURES

1. *Utricularia gibba* L. Portion of plant, about twice natural size.

2. Section of doorstep.

3. Diagram of section of doorstep. a, bifid hairs on inner slope of the step, b, the pad of modified hairs forming the doormat, c, the veil, d, slender hairs which are numerous in the vestibule, e, glandular hair of the outer wall.

4. A single bladder photographed: A. in the set condition, B. after tripping, C. after pricking the wall.

5. One-half of a doorstep viewed from above. To the left is shown the sloping portion merging with the lateral wall of the bladder, below is the inner edge of the step with its bifid hairs, above is the veil.

6. A bladder tripped in air, showing the air bubble swallowed by it.

7. Successive frames from motion picture. In the upper photograph the worm is outside the trap, in the lower it has been engulfed. Time interval about one-sixteenth of a second.

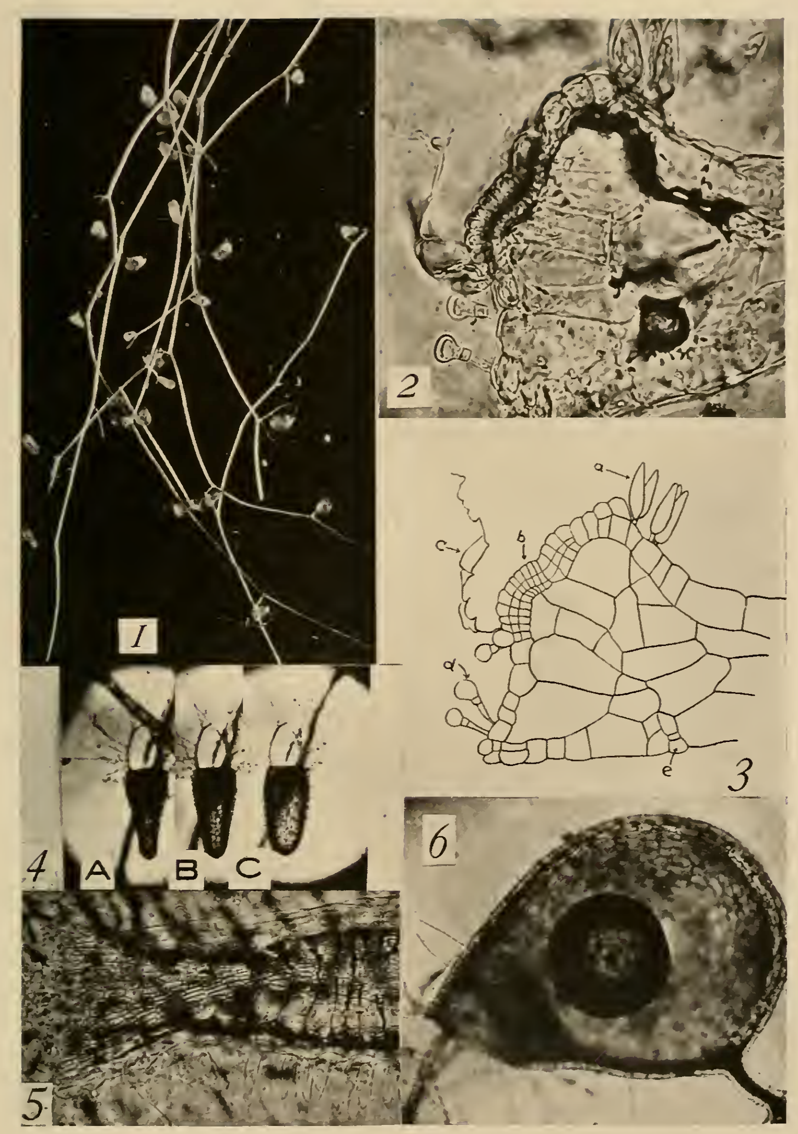
8. A detached trap that has swallowed a glass rod which tripped it.

9. In this case the door closed on a worm and jammed it against the doorstep.

10. A living trap viewed from the front to show the veil.

11. Anterior portion of bladder with part of the lateral wall cut away to show the door, the four trigger-hairs and the doorstep. Note the remains of a worm and a copepod.

12. Inner wall of bladder with quadrifid hairs.



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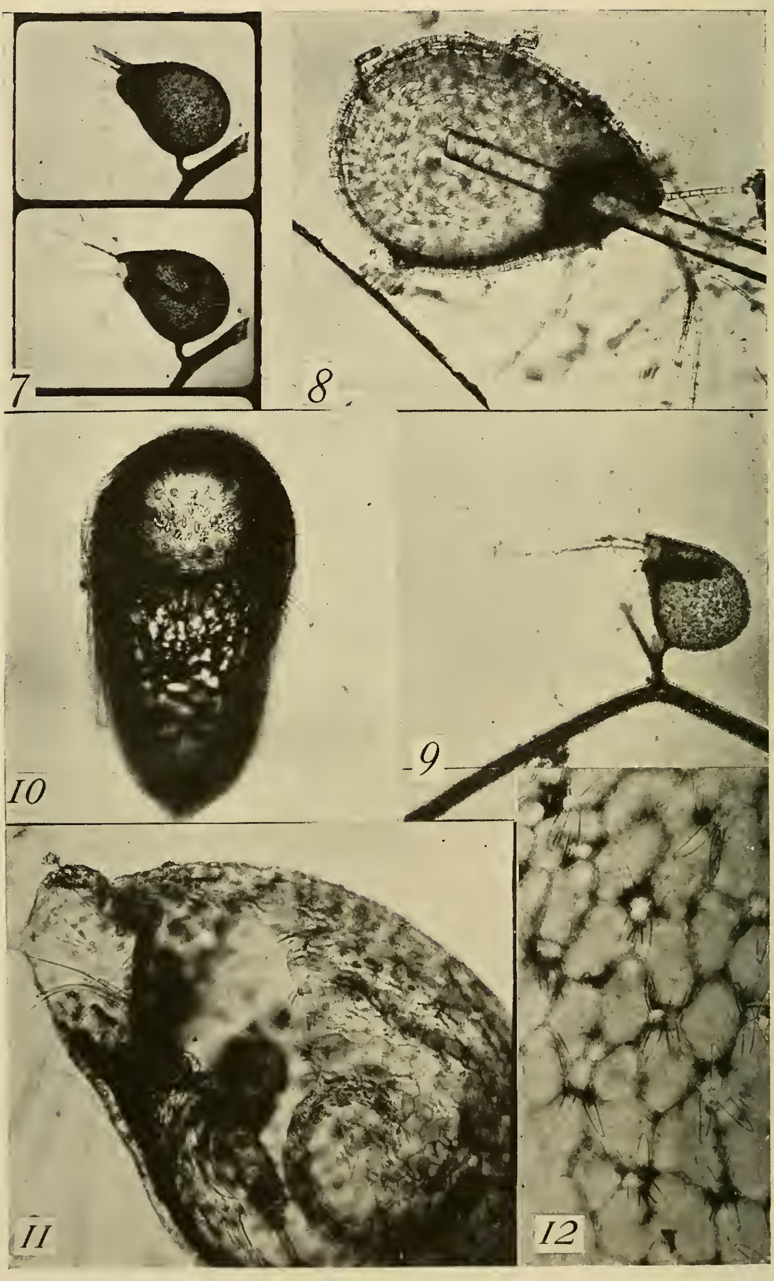

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